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Classification and Naming of Cat Retinal Ganglion Cells

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Abstract

Many schemes of ganglion cell classification seek to classify the cells by some particular characteristic, such as the time course of the cells' physiological responses or their dendritic morphology. It is here argued that such schemes are based on the Aristotelian concept of 'essences' and raise the same difficulties as have arisen with the essentialist approach to animal taxonomy. A better approach to the classification of neurones, it is proposed, is to base the classification on as many features of the cells as possible, and to regard the classification as an hypothesis, subject to testing and modification by experience, about the 'functional niches' occupied by the cell types distinguished.

Introduction

The problems faced by the neurobiologist in classifying nerve cells are in many ways the same as those faced by the animal or plant taxonomist in classifying organisms. This point has been made recently by TYNER [1975], who has directed attention to the potential value of taxonomic theory in the classification and naming of populations of neurones. In particular, his article drew to our attention an extensive literature on the history and logic of the classification of animals, and the relevance of that literature to issues which have arisen recently in the classification of retinal ganglion cells. Alternate ways of classifying and naming ganglion cells have recently been proposed by different workers, and the variety of names is potentially confusing to those not working in this particular area but interested nevertheless in following it. Just as importantly, the differences between the various schemes have proved sufficiently substantial to

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influence, and on occasions to confuse, subsequent work in visual neurophysiology.

One aim of this article, therefore, is to examine the logical presuppositions of different systems of ganglion cell nomenclature. A second aim is to use the conceptual framework provided by taxonomic theory to examine the logical and practical strengths of particular schemes of classification

proposed for cat retinal ganglion cells. Our third aim is the same as TYNER'S, to develop a theoretical basis for the classifying and naming of neurones which is relevant to any population of neurones, in any species.¹

Notes on Taxonomic Theory

Substantial discussions of taxonomic theory can be found in SIMPSON [1961] and MAYR [1969], and a cogent summary in TYNER'S article [1975]. The following points are particularly relevant to the present context.

(1) The method of classifying animals according to their 'essences', which stems from the Aristotelian and Platonic traditions, and which dominated all classificatory schemes until the 19th century, has been largely abandoned by modern taxonomists. Despite the development of authoritative schemes of classification for animals based on this method (such as the *Systema Naturae* of Linnaeus), many modern writers consider this approach to classification as 'not only totally inadequate but also highly inappropriate for modern taxonomy' [SIMPSON, 1961, p. 24].

(2) The reasons for this rejection of the Aristotelian approach by taxonomists are not specific to the problems of animal taxonomy. They have been summarised by (inter alia) SIMPSON [1961, chap. 1, p. 23], MAYR [1969] and TYNER [1975]. Briefly, to classify an object by this method its 'essence' must be identified correctly, and the identification of its essence means inevitably that other properties of the object are more or less explicitly declared to be non-essential or accidental. Not only is there rich

¹ Our debt to TYNER will be obvious throughout this article. Neither of us fully appreciated the relevance of taxonomic theory when we wrote the joint [WILSON *et al.*, 1976; ROWE and STONE, 1976a, b] and separate [STONE and FABIAN, 1966; LEICESTER and STONE, 1967; HOFFMANN *et al.*, 1972; STONE and HOFFMANN, 1972; STONE and FUKUDA, 1974a, b] papers in which the classification of ganglion cells or geniculate relay cells was an issue. Although we would not, had we appreciated the relevance of taxonomic theory, have diverted from the Y/X/W terminology and classification adopted in the above papers, we would have been able to provide a strong conceptual as well as empirical basis for their use and development.

ground for disagreement and divergence as to what is essential and what accidental, but the categorising of properties as 'accidental' has often downgraded interest in them, resulting, as TYNER [1975] expresses it, 'in much data being effectively discarded by either labelling atypical individuals "unnatural" or by creating for them new groups containing extremely small fractions of the total sample.' These difficulties have all arisen in recent schemes of ganglion cell classification, for the same reasons as they arose in the taxonomy of animals.

(3) Modern taxonomy has been greatly influenced by the theory of evolution, which has provided both a functional definition of a species (as a group of animals which interbreed freely with each other but which is reproductively isolated from all other groups, and therefore comprises an evolutionary unit), and a criterion for the classification of species into higher taxa (i.e., the criterion of common phylogenetic ancestry). Thus, evolution provided a much needed basis for defining categories of animals in terms completely

independent of the description of any particular group of animals, and made it possible to accommodate the descriptive variation which often exists within single natural groups of animals.

(4) Both because of the abandonment of the method of classifying animals by their essences, and because of the recognition of the importance of genetic composition for schemes of classification of biological populations, many modern taxonomists have adopted a multi-feature, 'polythetic' [TYNER, 1975] approach to classification. Because no feature can be regarded as self-evidently essential, many individual members of the subject population, and many features of each individual, should be surveyed; the survey of many features will at the same time allow a wide expression of a population's genetic composition to be taken into account. Conversely, a classification by many features can be readily adjusted to new accumulations of knowledge about the populations under study. Taken alone, this approach is purely empirical; its principal advantage is its compatibility with attempts to define biological groups according to functional criteria (such as evolutionary theory).

Classifications of Cat Retinal Ganglion Cells

Cat retinal ganglion cells have been classified both by their physiology and by their morphology, and several of the proposed schemes are set out in table I.

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Table I. Schemes of classification of cat retinal ganglion cells Physiological schemes

KUFFLER
ENROTH-CUGELL
SAITO *et al.*
CLELAND *et al.* [1971]
[1953]
and ROBSON
[1971]
CLELAND and LEVICK

[1966]
FUKADA [1971]
[1974 a, b]
type I type II
On-centre Off-centre
Y cells X cells

subsequently extended to

W cells .

by STONE and HOFFMANN [1972] and RODIECK [1973]
brisk-transient brisk-sustained

sluggish-transient sluggish-sustained

uniformity detectors local edge detectors colour-coded directionally selective edge-inhibitory off-centre

concentric

- non-concentric

Morphological schemes

LEICESTER and STONE [1967] SHKOLNIK-YARROS [1971] BOYCOTT and WASSLE [1974]

Multidendrite deep Multidendrite shallow Single dendrite loose Single dendrite dense Anomalous
bushy, sparsely branched bushy, densely branched large, horizontal broad small, horizontal broad
unilateral, horizontal broad central diffuse
a-cells (= Y cells) /?-cells(= X cells) y-cells (= W cells)

Physiological Schemes

The first description of the receptive field physiology of these cells was provided by KUFFLER [1953], who described two types of receptive field, those with On-centres and Off-surrounds, and those with Off-centres and On-surrounds. Subsequently, ENROTH-CUGELL and ROBSON [1966] described a different dichotomy of these cells and they termed the two classes that they distinguished Y and X cells. Each type included both On- and Off-centre types of receptive field; the two groups differed in their responses to drifting grating stimuli, in their receptive field size and retinal distribution and in the manner of summation by each cell of the influences

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of the centre and surround components of its receptive field (linear as against non-linear). Following fragmentary descriptions [RODIECK and STONE, 1965; STONE and FABIAN, 1966; RODIECK, 1967] of cells with receptive fields qualitatively different from those described by KUFFLER [1953], STONE and HOFFMANN [1972], STONE and FUKUDA [1974a] and FUKUDA and STONE [1974] presented evidence that a large minority of cat retinal ganglion cells are distinct from the cells KUFFLER [1953] described and/or from the X and Y cells described by ENROTH-CUGELL and ROBSON [1966]. Because of substantial properties common to these cells they were tentatively classed as a single group and were termed W cells, extending the Y/X terminology.

The term W cell was chosen because the alphabetical sequence W/X/Y then follows the increasing axonal velocities of the three types [RODIECK, 1973]. SAITO *et al.* [1971] and FUKADA [1971] saw two distinct types of cell which they termed type I and II. They have subsequently [SAITO and FUKADA, 1975] concluded that these are equivalent to Y and X cells and have adopted the latter terminology. CLELAND *et al.* [1971] also observed two types of ganglion cell, which they termed 'sustained' and 'transient'. Although considerable evidence has accumulated that these are equivalent, respectively, to X and Y cells, these workers [CLELAND *et al.*, 1976] still feel that it is premature to 'assert a one-to-one correspondence' between these pairs of classes, and have retained the sustained/transient terminology. To accommodate the cells

termed W cells by other workers, they distinguish 'brisk-sustained' cells (X cells) and 'brisk-transient' cells (Y cells) from 'sluggish-sustained' and 'sluggish-transient' cells which fall into the W cell grouping. Other cell types from the W cell grouping were characterised as 'non-concentric', but were given a variety of names and were granted the status of separate classes [CLELAND and LEVICK, 1974a, b] (table I).

HAMASAKI *et al.* [1973] proposed a type I/II dichotomy of cat retinal ganglion cells according to their responses to moving visual stimuli, and HICKEY *et al.* [1973] proposed a group I/II dichotomy according to the cells' responses to annular stimuli, both groups of workers suggesting that their cell groups were probably equivalent to the Y/X or transient/sustained groups. Because Kuffler's On-centre/Off-centre grouping is subsumed by subsequent groupings, and because SAITO and FUKADA [1975] have adopted the X/Y terminology, only two of the terminologies listed in table I are in common use: the W/X/Y terminology and the brisk/sluggish/sustained/transient/concentric/non-concentric terminology.

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Morphological Schemes

BROWN and MAJOR [1966] described a bimodality in the dendritic field size of cat retinal ganglion cells but did not explicitly suggest a classification of cells. LEICESTER and STONE [1967] described some diversity of dendritic morphology of these cells and attempted a classification by dendritic characteristics (number, density and depth of branching); they distinguished five groups. SHKOLNIK-YARROS [1971] suggested a seven group classification, relying principally on dendritic morphology. BOYCOTT and WASSLE [1974] proposed a 3-group classification which took into account dendritic morphology, soma and axon size, and retinal topography. This last classification (the *aply* classification) has been the most successful morphological approach and is the only grouping by morphology in common use.

Critique of Current Schemes of Ganglion Cell Classification

Physiological Schemes

The X/Y and sustained/transient schemes of classification deserve close comparison because they epitomise different, often conflicting, approaches to classification which have already emerged, interacted and, to a considerable degree, been sorted out in animal taxonomy. The comparison is best pursued with reference to the properties of these cells, as set out in table II.

X and Y Cells vs. 'Sustained' and 'Transient' Cells: A Question just of Terminology?

The differences between X and Y cells were first noticed by ENROTH-CUGELL and ROBSON [1966]. In order to measure the contrast sensitivity of individual ganglion cells to grating stimuli they devised an oscilloscope-based visual display, using which they

noticed striking evidence of a dichotomy among the sample of cells studied. The two sorts of cells were identified by their different responses to moving grating stimuli, but certain other distinguishing features were described. Thus, cells of one group responded to presentation of a stationary grating pattern in a way that suggested that the cell was summing the influences of centre and surround components of its receptive field non-linearly, while cells of the other group appeared to sum these influences approximately linearly, and the two groups of cells also differed in receptive field size and retinal distribu-

Classification of Neurones *Table II.* Some properties of cat retinal ganglion cells

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Y cells
X cells
W cells

small, $10^{-1}c$
large, $0.4-2.5^{\circ}$
linear
not tested
usually absent³
absent⁴
slow, 15–23 m/sec⁵ very slow, 2–18 m/sec⁶
medium, 14–22 /mi small, <15 /an
approximately 40 % approximately 50–55 %
to laminae A, Ai,¹¹ to SC¹⁸, to C-laminae and C¹² of LGN; of LGN and thence
to area 17;¹⁵ visual cortex area to midbrain (a minor- 17 and/or 18¹⁹, andity), but
probably 19²⁰
not to SC¹⁷
Receptive field centre size¹
Linearity of
centre-surround summation²
Periphery effect
Axonal velocity

Soma size,
peripheral retina⁷
Proportion of population⁸
Retinal
distribution

Central
projections

Nasotemporal division²¹
large, 0.5–2.5°

non-linear

present³
fast, 30°/sec⁵

large, >22 °/m

<10%

concentrate near area centralis, more numerous relatively in peripheral retina⁹
to laminae A, Ai,¹¹ and C¹² of LGN, to MIN¹³ and, via branching axon, to SC¹⁴
from the A-laminae of LGN to cortical areas 17 and 18¹⁵, also by branching axon; and
from MIN to areas 17, 18, 19¹⁶

nasal cells project contralaterally; most temporal cells ipsi-laterally; strip of intermingling
centred slightly temporal to area centralis

concentrate at area centralis⁹

nasal cells project contralaterally, temporal cells project ipsilaterally; narrow strip of
intermingling centred on area centralis

concentrate at area centralis and in streak¹⁰

nasal cells project contralaterally; most temporal cells also project contralaterally ;about
40 % of temporal cells project ipsilaterally
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Table II (continued)

Y cells
X cells
W cells

Responses to standing contrast

Receptive field 'layout'²⁶

Morphological²⁷ correlates
phasic or transient in most cells²², some are tonic or sustained especially near area centralis; all are tonic when dark adapted²³

On-centre/Off-surround
or
Off-centre/On-surround

a-cells
most give tonic responses in mesopic conditions²², either tonic or phasic²⁶, many are transient when light adapted²⁴

as for Y cells
some have same layout as Y and X cells; others have On-Off centres, some have purely inhibitory centres, some are directionally selective or colour-coded

y-cells
jg-cells

The superscripts refer to some important references on the properties listed, as follows.

¹ CLELAND and LEVICK [1974 a]; EN-ROTH-CUGELL and ROBSON [1966]; STONE and FUKUDA [1974a].

² ENROTH-CUGELL and ROBSON [1966].

³ CLELAND *et al.* [1971]; CLELAND and LEVICK [1974a].

⁴ CLELAND and LEVICK [1974a]; STONE and FUKUDA [1974 a].

⁵ BISHOP *et al.* [1953]; CLELAND *et al.* [1971]; FUKUDA [1971].

⁶ BISHOP *et al.* [1969]; STONE and HOFFMANN [1972]; STONE and FUKUDA [1974 a]; CLELAND and LEVICK [1974a].

⁷ BOYCOTT and WASSLE [1974]; CLELAND and LEVICK [1974 a]; CLELAND *et al.* [1973]; CLELAND *et al.* [1975]; FUKUDA and STONE [1974, 1975]; STONE and FUKUDA [1974b]; LEVICK [1975].

⁸ CLELAND and LEVICK [1974 b]; FUKUDA and STONE [1974]; ROVVE and STONE [1976b].

⁹ CLELAND *et al.* [1973]; ENROTH-CUGELL and ROBSON [1966]; FUKUDA and STONE [1974].

¹⁰ FUKUDA and STONE [1974]; ROWE and STONE [1976b].

¹¹ CLELAND *et al.* [1971]; HOFFMANN *et al.* [1972].

¹² CLELAND *et al.* [1971]; HOFFMANN *et al.* [1972]; CLELAND *et al.* [1976]; WILSON *et al.* [1976].

¹³ DREHER and SEFTON [1974]; MASON [1975].

¹⁴ HAYASHI *et al.* [1967]; HOFFMANN [1973].

¹⁵ STONE and DREHER [1973].

¹⁶ BURROWS and HAYHOW [1971]; GAREY and POWELL [1967].

¹⁷ CLELAND and LEVICK [1974a]; FUKUDA and STONE [1974].

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tion. ENROTH-CUGELL and ROBSON [1966] chose the non-descriptive labels X and Y for the two groups of cells. The term X cell was applied to cells which gave a modulated response to fine moving gratings, had linear summation properties and small receptive fields, and concentrated at the area centralis; the term Y cell was applied to cells which gave an unmodulated response to drifting gratings, had non-linear summation properties and large receptive fields and were most frequent in peripheral retina.

The choice of non-descriptive labels is noteworthy because it avoids in a simple way the use of the Aristotelian concept of

essences. The cells might, for example, have been termed 'linear' and 'non-linear', which would have implied that these features were their essential characteristics. With hindsight, it is apparent that the ability of the X/Y nomenclature to accommodate readily the considerable subsequent accumulation of knowledge about the variability present in the properties of X and Y cells stems principally from the fact that, while various features were of course attributed to cells of a particular label, no single feature was initially defined as essential to the dichotomy. The same advantages attended SATTO *et al.*'s [1971] choice of the non-descriptive labels types I and II and made easy their subsequent adoption of the X/Y terminology (which adoption has had a welcome, simplifying effect on the terminology in this area). CLELAND *et al.* [1971], CLELAND and LEVICK [1972, 1974a, b] chose, by contrast, to follow an essentialist approach. They recognised the X/Y differences described by ENROTH-CUGELL and ROBSON [1966] but, noting [CLELAND *et al.*, 1971] that 'the non-committal X/Y terminology ... does not convey the essential nature of the new classification', called them 'sustained' and 'transient' cells. They chose these terms because the responses of X cells to stationary contrast stimuli are tonic or sustained, i.e., they continue as long as the stimulus is presented, while the responses of Y cells are phasic or transient; and presumably these properties were con-

- ¹⁸ HOFFMANN [1973].
¹⁹ CLELAND *et al.* [1976]; WILSON *et al.* [1976].
²⁰ MACIEWICZ [1975]; LEVAY and GIL-
[1976].
²¹ STONE and FUKUDA [1974 b]; KIRK
[1976a, b].
²² CLELAND *et al.* [1971]; FUKUDA [1971].
²³ CLELAND *et al.* [1973]; ENROTH-
194 ROWE/STONE CUGELL and SHAPLEY [1973]; JAKIELA *et al.* [1976],
²⁴ JAKIELA *et al.* [1976].
²⁵ CLELAND and LEVICK [1974 a, b]; BERT
STONE and FUKUDA [1974a],
²⁶ CLELAND *et al.* [1971]; CLELAND *et al.*
[1974a, b]; ENROTH-CUGELL and ROB-
SON [1966]; STONE and FUKUDA [1974a].
²⁷ BOYCOTT and WASSLE [1974].

sidered to be 'essential' to the two cell types, in the Aristotelian sense. Conversely, these workers have argued [CLELAND *et al.*, 1975; LEVICK, 1975] that the X/Y terminology should be used only with respect to the linear/non-linear summation property originally described [ENROTH-CUGELL and ROBSON, 1966]. Thus, they seem to have interpreted the earlier paper as defining linearity of summation properties as the 'essence' of the X/Y classification, even though this definition was not proposed explicitly in the original paper, and the choice of non-committal labels (X/Y) suggests that it was also not intended.

The sustained/transient classification has raised many of the problems which beset the 'essential feature' approach to the taxonomy of animal species. First, there is little apparent justification for the choice of the sustained or transient nature of X and Y cell responses as more essential to the cell types than several other properties, which seem at least as important in understanding their function - such as the central projections of their axons, their retinal distribution and their relative numbers (table II). It could, in

fact, be cogently argued that any of these latter features is more important than the sustained/transient difference. The sustained/transient difference is commonly not apparent in a cell's response until 1–2 sec after the presentation of a stimulus to a ganglion cell in a paralysed eye, and there is evidence [PRITCHARD and HERON, 1960; HEB-BARD and MARG, 1960; WINTERSON and ROBINSON, 1976] that, unpara-lysed, a cat's eyes do not stay still for periods sufficiently long to permit the brain to see this difference. For example, PRITCHARD and HERON [1960] describe constant drifting-movements of the cat's eyes of $0.5^\circ/\text{sec}$ mean velocity, and WINTERSON and ROBINSON [1976] describe similar movements of approximately $0.25^\circ/\text{sec}$ mean velocity, in addition to tremor and saccadic movements.

Second, it was noted that the sustained/transient nature of a cell's responses to visual stimuli could not be used as a reliable diagnosis of cell type. DUBIN [1974] noted, for example, that many 'transient' cells have a weak but clear sustained component to their responses. CLELAND *et al.* [1973], ENROTH-CUGELL and SHAPLEY [1973] and JAKLELA *et al.* [1976] noted that the responses of Y cells become quite tonic when the retina is dark-adapted, and JAKDSLA *et al.* [1976] noted a tendency for X cells to give transient responses when light-adapted. CLELAND and LEVICK [1972] commented (in answer to a question in discussion) that any one of the receptive field tests they applied to distinguish the two cell types, including presumably the sustained/transient test, was unreliable in up to 20% of

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cases, but that on the basis of other tests cells could be reliably classified. This suggests that the sustained/transient difference is in fact not essential to the sustained/transient classification, and that, on the basis of other properties, cells giving transient responses might be classified as 'sustained', and vice-versa.

Further, the choice of the descriptive terms 'sustained' and 'transient' where X and Y might have been used has led to some confusion in subsequent work. SHAPLEY and HOCHSTEIN [1975] emphasised that cells whose responses were respectively sustained and transient do not (at least in the lateral geniculate nucleus) correspond to linear and non-linear cells, and IKEDA and WRIGHT [1976] have recently presented a paper entitled 'Properties of sustained X cells, transient Y cells and transient X cells in the cat's lateral geniculate nucleus', making the same point that SHAPLEY and HOCHSTEIN [1975] had made. IKEDA and WRIGHT [1974] had earlier criticised a view expressed by HOFFMANN and STONE [1971] that some of the differences between the so-called 'simple' and 'complex' cells of cat visual cortex were determined by whether they received input from X or Y type retinal ganglion cells. Their criticism was based on the observation that simple cells were not always sustained, and complex cells were not always transient in their responses. This criticism involves an over-simplification of HOFFMANN and STONE'S conclusion, but, even if it did not, the criticism could be valid only if a sustained or transient response is both a reliable and essential characteristic of, respectively, X and Y

cells. It now seems to be appreciated that it is neither of these things. This sort of problem simply did not arise when a non-descriptive terminology was used.

Thus, the choice between the X/Y and sustained/transient terminologies is not simply a matter of which label to apply. Issues such as the use or avoidance of the Aristotelian concept of the 'essential nature' of a cell group are involved, as well as the ability of a scheme of classification to assimilate and adapt to new data. The sustained/transient terminology can still be used if it is kept in mind, and explained to each newcomer in the field that the terms mean both less and more than they seem to; that 'sustained' cells commonly give transient responses, and vice versa, and that many other equally or more important properties are subsumed, and tend to be obscured, by these labels. Following the taxonomists' experience, the X/Y classification seems both simpler and more adaptable than the essentialist approach. Most of the problems raised by the essentialist approach to ganglion cell classification, stem from the emphasis this ap-

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proach places on one or a few properties of the cells, and are therefore avoided if a terminology and classification are used which can take into account many features of the cells. As TYNER (1975) has commented 'this polythetic view ... offers several advantages ... Most importantly, its use reduces the tendency to focus attention on one or a few currently intriguing features which may later prove unreliable, unimportant, or difficult to observe under certain circumstances.'

W Cells vs. Sluggish Concentric and Non-Concentric Cells: A Question of Classification

The emergence in studies of cat ganglion cell physiology of cells clearly different from X and Y cells required users of both the terminologies discussed above to develop a new term or terms. STONE and HOFFMANN [1972] and RODIECK [1973], noting a number of features common to these cells (table II), grouped them together and chose a term 'W cell' which was an extension of the original X/Y terminology and had a systematic relationship to it (see above). Subsequent studies [STONE and Fu-KUDA, 1974a, b; FUKUDA and STONE, 1974; WILSON and STONE, 1975; WILSON *et al*, 1976; ROWE and STONE, 1976b] have increased the number of properties known to be common to W cells [summarised in ROWE and STONE, 1976b], and hence have expanded the basis for grouping them together.

CLELAND and LEVICK [1974a, b] by contrast, continued with an essentialist approach by setting out two new essential features of retinal ganglion cells. First, they divided the newly recognised cells (W cells) into 'concentric' and 'non-concentric' types. A concentric receptive field, as defined by these workers, has an On-centre and Off-surround or an Off-centre and On-surround (receptive fields with, for example, an On-Off centre and a concentric, purely inhibitory surround are termed 'non-concentric', although in fact

they are concentrically organised). The 'concentric' or 'non-concentric' organisation of a receptive field was considered a 'key property' [LEVICK, 1975], although no justification has been presented for considering it important. Second, because the originally recognised 'sustained' and 'transient' cells were concentric in this sense, and the concentric varieties of the new cells were also to be classified as 'sustained' or 'transient', a further essential feature had to be introduced. It was noted that the peak firing rates of the various cells to optimal visual stimuli were higher among the original sustained and transient cells (i.e., in X and Y cells). These were termed 'brisk-sustained' and 'brisk-trans-

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sient' cells, respectively, and the newly recognised 'concentric' cells were termed 'sluggish-sustained' and 'sluggish-transient'. The 'non-concentric' varieties of new cells were also given a variety of descriptive names, such as uniformity-detector (i.e., a cell considered specialised to respond to uniformity in the retinal image), and local-edge detectors (cells considered specialised to respond to edges within a particular region of the visual field). Altogether seven categories were set up to deal with cells elsewhere grouped into the single W cell category, some categories containing less than 1% of cells in the overall sample of neurones. Following the taxonomist's experience [TYNER, 1975], the essentialist approach to classification had led to the setting up of numerous classes of cells, some containing only a small fraction of the population.

The sluggish / brisk / sustained / transient / concentric / non-concentric scheme for classifying cells is obviously more cumbersome verbally than the Y/X/W scheme. The expanded set of descriptive terms might be valuable if they either avoided problems raised by the simpler non-descriptive terminology or illuminated relationships which were otherwise obscured. Yet the opposite seems to have been the case. Thus, the only criticisms so far expressed of the W cell grouping are that 'W cells have in common only that they are not X or Y cells' [CLELAND and LEVICK, 1974a] or that 'about the only common feature of W cells is the possession of a thin axon and slowly-conducted impulses' [LEVICK, 1975]. Both statements overlook many substantial features common to W cells; these are included in table II and are summarised by ROWE and STONE [1976b]. Conversely, the essentialist terminology has obscured important relationships and similarities between cell types, because it defined certain features of the cells to be essential. For example, the 'sluggish transient' cells were regarded as quite distinct from 'local-edge detectors', and indeed are described in different papers [CLELAND and LEVICK, 1974a, b]. However, STONE and FUKUDA [1974a, b] noted a considerable similarity between these cells in their visual responses, axonal conduction velocity, and pattern of naso-temporal division, and described the existence of cells with properties intermediate between the two types. This suggested that these receptive field types might form a natural continuum, and recognition of such a continuum tends to

reduce and simplify the number of varieties of cell contained within the W cell grouping. This relationship did not emerge from CLELAND and LEVICK'S description because they considered the 'concentric'/'non-concentric' organisation of a receptive field an essential feature. Again, all W cells, the 'non-concentric' as well as the 'concentric'

are 'sluggish' in their visual responses; yet CLELAND and LEVICK'S classification obscures this common property, because they applied the term sluggish only to the 'concentric' W cells. Presumably they considered the 'non-concentric' feature of the other W cells to be their essential feature. Yet again, CLELAND and LEVICK [1974b] have subdivided the 'suppress-ed-by-contrast' type of W cell described by RODIECK [1967] and STONE and HOFFMANN [1972] into two distinct sub-types ('uniformity detectors' and 'edge inhibitory Off-centre' cells), but we [ROWE and STONE, 1976b] could not confirm the dichotomy. There seemed in this case, too, to be a continuum of properties.

In short, the Aristotelian essentialist approach, by creating sharp categories of cells, tends to make divisions among them which may be artificial. This tendency has been previously noted in the taxonomy of animals. Thus, MAYR [1969, p. 67] comments that 'this philosophy... attempts to assign the variability of nature to a fixed number of basic types... It postulates that all members of a type reflect the same essential nature. This is why the essentialist idea is also referred to as typological. Variation, consequently, is considered by the typologist as trivial and irrelevant. The constancy of taxa and the sharpness of the gaps separating them tend to be exaggerated by him. The fatal flaw in essentialism is that there is no way of determining what the essential properties of an organism are and why these and no other properties are essential.'

Morphological Classifications

The *alfily* cell classification proposed by BOYCOTT and WASSLE [1974], although the newest of several morphological classifications, has already had more impact than those that preceded it. The reason is twofold. On the one hand, the earlier classifications, including that proposed by one of us [LEICESTER and STONE, 1967], were essentialist in character. LEICESTER and STONE'S classification, for example, turned entirely on dendritic morphology. Small groups of cells were set up to cope with some of the variety of dendritic morphology observed ('shallow', 'anomalous') and no account was given to other features of cell morphology, or to retinal topography. The names chosen for the groups were descriptive and essentialist. The *aiipy* classification, by contrast, is carefully stated to avoid any commitment to a particular feature. It takes into account soma size, dendritic morphology, axon size, and, a previously neglected parameter, retinal topography. It is a simpler classification than any previous one, yet more powerful. The second reason for its wide acceptance was its ob-

vious compatibility with physiological groupings, most simply with the Y/X/W grouping [BOYCOTT and WASSLE, 1974]. Like the latter grouping it can accommodate new findings and diversity within present classes although the recognition of new classes is not excluded.

Description and Definition; Identification and Classification In general, the problems raised by the essentialist approach to ganglion cell classification are of two types. Each is relevant to classifications based both on morphology and physiology. The first problem is the tendency of the essentialist approach to make no distinction between description and definition. In animal taxonomy, this distinction is embodied in the distinction between taxa and categories [BOCK, 1973; see below]. Categories, such as family or species, can be defined, but taxa, such as *Feli-dae* or *Felis domesticus*, may only be described. The essentialist approach to classification does not provide any basis for this distinction, and this is often a source of confusion. For example, as mentioned previously, CLELAND and LEVICK have argued [CLELAND *et al.*, 1975; LEVICK, 1975] that the X/Y terminology should be used only with reference to linear or nonlinear summation properties, thus regarding these characteristics as definitions of the two cell types, and giving them the dual status of categories as well as taxa. As already noted, such definitions do not appear to have been proposed in the original papers and there is little justification for now introducing them. ENROTH-CUGELL and ROBSON [1966, p. 547] comment that 'Whether our classification of ganglion cells into two distinct classes would be upheld by objective measurements of the detailed behaviour of a large sample of ganglion cells under a wide range of conditions ... cannot be answered.' These two groups of cells were identified in a limited sample of cells (128) by a particular criterion (response to a drifting grating) and a correlation was described between this response and several other properties (linearity of response to stationary grating, receptive field size, retinal distribution and, possibly, axon size). Taxon-omic categories were not defined for these cells in terms of any one of these criteria.

CLELAND and LEVICK'S assumption that a definition had been laid down, clearly stems from a philosophical approach which tends to equate description with definition. POPPER [1962, p. 34] in describing the essentialist approach to classification, remarks that all essentialists, including Aristotle 'agreed with Plato in determining the task of pure knowledge as the discovery of the hidden nature or form or essence of things. All these

methodological essentialists also agreed with Plato in holding that these essences may be discovered and discussed with the help of intellectual intuition; that every essence has a name proper to it, the name after which the sensible thing is called; and that it may be described in words. A description of the essence of a thing they

called a "definition". Since linear and non-linear summation are mutually exclusive categories, if it is insisted that X and Y cells have been, or should now be, defined as comprising, respectively, all linear and all non-linear retinal ganglion cells, then arguably there can be only two categories of retinal ganglion cell, and the X/Y terminology cannot deal with newly recognised cell groups except by regarding them as varieties or subtypes of X and Y cells. The alternative, non-essentialist approach is to regard the linear or non-linear summation properties of X and Y cells as only one of their properties, rather than as a definition of their respective categories. The recognition of other categories, or of groups of cells clearly distinct from the originally described X and Y cells in properties other than linearity of summation then becomes possible, and does not require the abandonment of the X/Y classification.

T. The second problem is the tendency of the essentialist approach to equate identification with classification. Mayr [1969] and Tyner [1975] have recently stressed that these are quite distinct operations Mayr [1969

p. 66] commenting that 'Unlike identification which deals with a few characters (ideally a single one) that throw a given specimen into one or the other line of the key classification deals with and evaluates a multitude of characters ideally all of them.' The process of classification is inductive. After examination of a wide variety of properties in a sufficiently large sample of cells (ideally all cells)

a classification of the cells into groups can be arrived at inductively by generalizing from particular observations. A given cell can then be identified by a particular feature as a member of a certain group but logically this process of identification is deductive. Often however

the essentialist both classifies and identifies by the possession of one or a few essential features. For example. '... attention will be confined to a subset of the properties by which a neurone may be rapidly put in one or other class. On the basis of the tests applied it would be more appropriate to speak of a sustained/transient rather than an X/Y classification since the nature of the responses to standing contrast is one of the principal distinguishing features.'

[Cleland et al

1971

p. 474]. This approach clearly results in the loss of the distinction between identification and classification. Mayr [1969

p. 66] comments